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Was Lamarck's evening primrose (*Oenothera Lamarckiana* Seringe) a form of Oenothera grandiflora Solander?

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(WITH PLATES 37–39)

This paper will present evidence which in the writer's opinion clearly indicates that the *Oenothera* grown in the gardens of the Muséum d'Histoire Naturelle at Paris about 1796, described by Lamarck (?1798) under the name *Aenothera grandiflora* and renamed by Seringe (1828) *Oenothera Lamarckiana*, was a form of *Oenothera grandiflora* Solander (1789), introduced into England in 1778 from Alabama. If this identification is correct it follows that the name *Oenothera Lamarckiana* Seringe becomes a synonym of *Oenothera grandiflora* Solander (*O. grandiflora* "Aiton").

The evidence in the light of recent studies shows that Professor De Vries made an incorrect determination of the material of his cultures when he identified it with Lamarck's plant of 1796 or earlier. The material of De Vries's cultures is very different from this plant and can only be allowed to keep the name *Lamarckiana* when written "*Oenothera Lamarckiana* De Vries"; it is not *Oenothera Lamarckiana* Seringe.

My attention was first directed to this matter on seeing in the herbarium of the New York Botanical Garden tracings of Lamarck's plant, the type of *Oenothera Lamarckiana* Seringe, which is preserved in Lamarck's herbarium at the Muséum d'Histoire Naturelle. The resemblance of these tracings to the material of *Oenothera grandiflora* Solander from Alabama, now assembled in

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my own collections and at the New York Botanical Garden, was unmistakable. Miss Alice Eastwood, who kindly looked up various matters for me during her recent trip abroad, examined last winter in Paris this sheet which stands for the type of *Oenothera Lamarckiana* Seringe and reported to me her belief that it is identical with *O. grandiflora* Solander. As a result of this report I obtained through the courtesy of M. François Gagnepain negatives of this and other herbarium sheets at the Muséum d'Histoire Naturelle bearing upon the problem. M. Gagnepain further has most kindly answered a number of specific enquiries concerning the history of the specimens and certain characters of the plants not shown in the photographs. The following descriptions of these herbarium sheets are then in part from the photographs here published and in part from the notes of Miss Eastwood and M. Gagnepain, to whom I am greatly indebted.

The three sheets, to be described, were examined by Professor De Vries, who has given his interpretation (1901) in footnotes to Die Mutationstheorie, Vol. I, pp. 316, 317. De Vries believed that the first two sheets agreed with his cultures of *Lamarckiana*. The specimens on the third sheet he referred to *Oenothera grandiflora* Aiton (*O. suaveolens* Desfontaines) = *O. grandiflora* Solander. The conclusions of the present paper are (1) that the first sheet (PLATE 37), the type of *Oenothera Lamarckiana* Seringe, shows a remarkably well preserved and characteristic specimen of *Oenothera grandiflora* Solander, (2) that the specimen on the second sheet (PLATE 38) is neither *O. grandiflora* Solander nor "*O. Lamarckiana* De Vries" but a plant that is close to certain forms of *O. biennis*, and (3) that the two plants on the third sheet (PLATE 39), obviously stunted in growth, are so imperfect that an opinion of their identity can hardly be more than a guess. Our interest in this herbarium material centers upon the first two sheets.

SHEET 1. LAMARCK'S PLANT, WHICH STANDS AS THE TYPE OF *Oenothera Lamarckiana* Seringe

This specimen (PLATE 37) is in the herbarium of Lamarck, acquired by the Muséum d'Histoire Naturelle in 1886. The sheet bears in the handwriting of Lamarck: "Oenothera . . . [grandiflora] . . . nova spec. flores magni lutei, odore grato, caulis

3 pedalis." The spelling of the word Oenothera is not clear; it might be interpreted "Onothera" or possibly "Aenothera." This note designating a new species, *grandiflora*, in the handwriting of Lamarck establishes the specimen as what we would now designate as the type of his species *Aenothera grandiflora* described in the Encyclopédie Méthodique Botanique **4**: 554. ?1798. This description agrees with the specimen. It seems unlikely that we shall ever know the exact date at which the description was published. Authors usually give it as 1797, but Sherborn and Woodward (1906), from evidence presented by extraneous matter bound in with certain copies of the volume concerned, place the year as ?1798. I can find no evidence that Poiret wrote the description, as was believed by De Vries, but he is known to have written later volumes of the encyclopedia.

Seringe in his diagnosis of *Oenothera Lamarckiana* (De Candolle, Prodromus **3**: 47. 1828) gives *O. grandiflora* Lamarck as a synonym together with the comment that the species is not the *grandiflora* of Aiton. This was of course his reason for renaming the plant. The diagnosis of Seringe, as will appear later, is virtually a copy of a portion of Lamarck's description.

The following is the description of the species written by Lamarck in the Encyclopédie Méthodique Botanique; it should be noted that the abbreviation (V.S.) at the end of the diagnosis shows that the description was based on dried material.

"12. Onograire à grandes fleurs. *Ænothera grandiflora* (n). *Ænothera foliis integerrimis, ovato-lanceolatis; petalis integris, capsulis glabris.*

"Cette espèce paroît se rapprocher, par son port, de l'*ænothera longiflora;* mais elle en diffère par plusieurs caractères frappans, sur-tout par ses tiges rameuses, ses pétales entiers, ses fruits lisses & courts.

"Ses tiges s'élèvent à trois ou quatre pieds de hauteur. Elles sont cylindriques, munies de quelques poils rares, d'un rouge brun, divisées en rameaux nombreux, étalées. Les feuilles sont vertes, alternes, ovales, lancéolées, lisses & glabres des deux côtés, très-entières; les feuilles du bas sont pétiolées & munies de quelques dents à peine sensibles. Celles qui accompagnent les fleurs sont plus étroites, plus aiguës & sessiles.

"Les fleurs sont terminales, & forment, par leur disposition, une panicule étalée; elles sont axillaires, solitaires, mais très-

rapprochées. Le calice est jaune, muni d'un tube un peu plus long que la corolle, qui se divise en quatre folioles lancéolées, élargies à leur bâse, aiguës à leur sommet, terminées par un filet court, sétacé. La corolle est jaune, composée de quatre pétales ovales, très-grands, entiers, arrondis, presque aussi longs que le tube calicinal, retrécis à leur bâse en forme de coin. Les anthères sont longues, linéaires. Le fruit est une capsule courte, cylindrique, glabre, tronquée, légèrement quadrangulaire, n'ayant qu'environ le tiers de longueur du tube calicinal. Cette espèce est originaire de l'Amérique septentrionale. On la cultive au jardin du Muséum d'Histoire naturelle. (V.S.)"

An interesting point has been brought to my notice by Mr. H. H. Bartlett. Poiret has this note in the Encyclopédie Méthodique Botanique, Suppl. **4**: 141. 1816: "L'Oenothera grandiflora, no. 11, est la même plante que celle d'Aiton, Hort. Kew., 2, pag. 2." The designation "no. 11" instead of "no. 12" must have been a slip of the pen on Poiret's part. Although Poiret was correct in considering *O. grandiflora* Lamarck as a synonym of *O. grandiflora* Solander, he could not have had a clear conception of this plant since he kept *O. suaveolens* Desfontaines, which is also a synonym, as a distinct species.

We will give also the short diagnosis by Seringe (1828) of *Oenothera Lamarckiana* for comparison with the longer description of Lamarck.

"OE. Lamarckiana (Ser. mss.) caule ramoso, *foliis integerrimis ovato-lanceolatis, petalis integris* magnis, *capsulis glabris* cylindrico-tetragonis brevibus. ② in Americâ sept. OE. grandiflora Lam. dict. 4. p. 554. *non Ait. Fl. flavi."

I have italicized phrases that are the same as those in the brief introduction in the description of Lamarck, showing that Seringe had little or nothing to add to the original description.

Certain points should be noted in these descriptions of Lamarck and Seringe before we compare Lamarck's plant (PLATE 37) on the one hand with *O. grandiflora* Solander and on the other with the material of De Vries's cultures ("*O. Lamarckiana* De Vries"). The description of the petals as entire must not be emphasized, for while there may not be in these species a conspicuous notch at the tip of the petals there is usually at least a shallow indentation; the character is not one easily determined in dried specimens and

presents so much variation as to have no taxonomic value. The leaves of these species are not strictly entire but serrulate, the teeth being small and in dried material inconspicuous; the teeth are, however, shown on some of the leaves on Lamarck's plant (PLATE 37). The glabrous fruits agree best with the seed capsules of *grandiflora*, which are almost smooth, while those of De Vries's *Lamarckiana* are decidedly puberulent and pilose. Mature capsules are not shown on the specimen of Lamarck's plant, and no importance can be attached to their description as short. The reddish brown stem with occasional hairs agrees with *grandiflora*; there is no mention of numerous hairs arising from red papillae, a striking characteristic of the plants in the cultures of De Vries. The description of the leaves as glabrous is not strictly true either of *grandiflora* or of De Vries's *Lamarckiana*, both having a minute pubescence, which is more evident in the latter form. Mr. Bartlett has called my attention to the word "sétacé" in Lamarck's description of the sepal tips; this has been translated by De Vries (1901, p. 317) as "dicke." The French is, however, from the late Latin word "setaceus," derived from "seta," a stiff hair or bristle. The meaning is, then, exactly the opposite of that given by De Vries and refers to the much attenuated sepal tips, as shown in PLATE 37, a striking characteristic of *grandiflora;* the sepal tips of De Vries's *Lamarckiana* are in contrast much shorter and thicker.

It is surprising how little information is contained in the descriptions of Lamarck and Seringe that is of value in a comparison of Lamarck's original plant with *O. grandiflora* Solander and "*O. Lamarckiana* De Vries." The most important points in the writer's opinion are the description of the attenuated sepal tips and the absence of all reference to the remarkable stem coloration which is characteristic of the material of De Vries's cultures. De Vries's *Lamarckiana* invariably, so far as I am aware, presents a green stem punctate with red papillae from which long hairs arise among a short glandular pubescence. This is not noted by Lamarck, who describes the stem in agreement with *grandiflora* as reddish brown with occasional hairs.

We may now take up the consideration of the herbarium sheet of Lamarck's plant (PLATE 37) preserved in the herbarium of the

Muséum d'Histoire Naturelle. First, however, it should be noted that Buchet (1912) in a recent paper gives his opinion that this sheet agrees with *Oenothera suaveolens* Desfontaines, which he recognizes as synonymous with *Oenothera grandiflora* Solander, an older name. Buchet also regards the sheet shown on PLATE 38 from the collection of Abbé Pourret as the same form as Lamarck's plant and identifies it also with *O. suaveolens*. On this point I cannot agree, since, as will be shown later, the specimen of Abbé Pourret has important characters that distinguish it both from Lamarck's plant (*O. suaveolens* Desfontaines = *O. grandiflora* Solander) and from the material in the cultures of De Vries.

In the following account of the sheet which stands for the type of *Oenothera Lamarckiana* Seringe, are included not only the characters shown by the photograph (PLATE 37) but also others of equal or perhaps greater importance from the notes of Miss Eastwood and M. Gagnepain. In order to obtain direct comparisons with respect to the pubescence I furnished M. Gagnepain with specimens of stems and buds from both *grandiflora* and the *Lamarckiana* of De Vries's cultures, asking him to compare the specimens with Lamarck's plant but not informing him of their source.

1. STEM AND FOLIAGE. The specimen of Lamarck's plant (PLATE 37) exhibits the rather dense branching characteristic of certain forms of *grandiflora* in sharp contrast to the long sparsely branched stems of De Vries's *Lamarckiana*. The stem, according to M. Gagnepain, does not have long hairs from red papillae, as is so characteristic of De Vries's *Lamarckiana;* the pubescence is short and the stem subglabrous. The leaves are broadly elliptical or lanceolate with serrulate margins and with short but distinct petioles as in *grandiflora;* they are not sessile or almost sessile nor so broad as are the leaves of the *Lamarckiana* of De Vries. This herbarium sheet may be readily matched in the form of the branching and in the foliage by numerous specimens of *grandiflora* collected in Alabama; it represents neither the broader- nor the narrower-leaved forms in the range of variation in this species but is nearest to the intermediate condition.

2. INFLORESCENCE. The inflorescence does not present the close spike with broad-based, sessile bracts, which are so character-

istic of the younger flowering shoots of De Vries's *Lamarckiana*. On the contrary the bracts are narrow and short-petioled and the inflorescence is more open, in agreement with *grandiflora*.

3. BUDS. The buds are not stout as in the *Lamarckiana* of De Vries and the sepal tips are much more attenuate, a distinctive character of *grandiflora*. The form of the buds is exactly as in *grandiflora*, and this character is one of the most important points of agreement with this species. The pubescence on the sepals, as described by M. Gagnepain, is short; there are not present the numerous long hairs from papillae, which are characteristic of De Vries's *Lamarckiana*.

4. FLOWERS. The flowers have the very long and delicate hypanthium characteristic of *grandiflora*. Miss Eastwood reports that the petals in a bud dissected by her are entire. This is a character typical of neither *grandiflora* nor the *Lamarckiana* of De Vries, but as stated before, the petals of these forms vary so greatly in the degree of their indentation that the character has little if any taxonomic value. The length of the petals, between 3 and 4 cm., is that of *grandiflora* and also of certain forms of De Vries's *Lamarckiana*. The style extends beyond the tips of the anthers so that the lobes of the stigma (*s*, in PLATE 37) are above the latter and could not be pollinated in the bud. In these respects the flower agrees with both *grandiflora* and the large-flowered types of *Lamarckiana* in De Vries's cultures.

5. CAPSULES. There are apparently no mature capsules on the specimen, so direct comparisons are impossible. Since the size and form of a capsule depends upon the development of the ovules, i. e. upon whether or not the stigma has been fully pollinated, it is unsafe to accept statements of size unless there is evidence that sufficient material has been examined. Lamarck's statement that the capsules are short was probably based on immature or partially pollinated capsules. His description of the capsules as glabrous points to *grandiflora;* as stated before, the capsules of De Vries's *Lamarckiana* are decidedly puberulent and pilose.

The characters of *Oenothera grandiflora*, which appear on the herbarium sheet of Lamarck's plant, and those of the *Lamarckiana* of De Vries's cultures may be more readily contrasted in the following statement.

O. grandiflora Solander AND LAMARCK'S PLANT	*O. Lamarckiana* FROM THE CULTURES OF DE VRIES
Flowering stems generally with numerous approximate branches.	Flowering stems sparsely branched or not at all.
Stems green above, reddish brown below, the papillae at the base of long hairs colored like the stem.	The papillae at the base of the long hairs colored red so that the green stem appears punctate with red dots.
Leaves of upper foliage lanceolate, rarely broad, with distinct petioles.	Leaves of upper foliage ovate-lanceolate, sessile or almost sessile.
Inflorescence more open, with narrow, petioled bracts.	Inflorescence more close, with sessile bracts broad at the base.
Buds not stout, with much attenuated sepal tips. Sepals puberulent, sometimes sparsely pilose.	Buds stout, with shorter sepal tips. Pubescence of sepals a heavy puberulent and pilose covering.
Flowers with a long delicate hypanthium. Petals 3–3.5 cm. long. Stigma lobes above the tips of the anthers.	Flowers with a stouter hypanthium. Petals in some races 4–4.5 cm. long, in others 2.5–3 cm. long. Stigma lobes in the large-flowered types above the tips of the anthers, in the smaller-flowered forms at about the level of of the anther tips.

There is another sheet in the herbarium of the Muséum d'Histoire Naturelle which is without a name but bears in the handwriting of Lamarck: "d'Amérique sept. Tige rameuse, haute de 3 à 4 pieds." Both M. Gagnepain and Miss Eastwood report that this sheet is similar to that of Lamarck's plant which we have described above and shown on PLATE 37. The history of the sheet is apparently not known and I have no evidence that it can safely be associated with the specimen upon which Lamarck undoubtedly based his description. Nevertheless, this sheet may be closely related to or even a duplicate of the specimen that served as the type for the descriptions of Lamarck and Seringe.

In summary it may be said that the specimen, which we must consider the type of *Oenothera Lamarckiana* Seringe, presents no characters in clear form that are not those of *O. grandiflora* Solander. In not one of the contrasted characters discussed above does the specimen agree with the *Lamarckiana* of De Vries's cultures. The only points in which De Vries's *Lamarckiana* may be said to resemble this specimen are the size of the petals and the position of the stigma, which in the large-flowered forms of *Lamarckiana* is above the tips of the anthers; these are characters which *grandiflora* and De Vries's *Lamarckiana* have in common.

It is exceedingly fortunate that the plant which serves as the type of *Oenothera Lamarckiana* Seringe should have come down to us so well preserved that there is scarcely a doubt of its identity with *Oenothera grandiflora* Solander, introduced into England in 1778.

SHEET 2. A SPECIMEN OF *Oenothera* FROM THE COLLECTION OF ABBÉ POURRET

This specimen (PLATE 38) is of interest for the reason that De Vries (1901, footnote to p. 317) believed that it as well as Lamarck's plant agreed with the material of his cultures ("*Oenothera Lamarckiana* De Vries"). Buchet (1912) has recently referred the specimen to *Oenothera suaveolens* Desfontaines = *O. grandiflora* Solander. I am unable to agree with either of these opinions and shall present evidence that the plant was close to certain forms of *Oenothera biennis*.

The sheet bears the label HERB. MUS. PARIS. with the statement at the bottom "Collection de l'Abbé Pourret, extraite de l'Herbier légué par M. le Dr. Barbier. 1847." On this label, in the handwriting of Spach are the names "*Onagra vulgaris* Spach" and "*Oenothera biennis* Linné." At the left is a list of old names representing synonymy, copied by Abbé Pourret, and below this list his clerk wrote the name *Oenothera biennis* L.

De Vries states that the plant was probably collected by Abbé Pourret in the garden of the museum at the time of his visit to Paris in 1788. M. Gagnepain, however, is not satisfied with the evidence for this view and writes that the history of the sheet is unknown to him.

An examination of the specimen itself (PLATE 38) shows the following characters.

1. STEM AND FOLIAGE. The long unbranched stem bears elliptical, petioled leaves very different from the sessile or almost sessile, broad-based leaves of De Vries's *Lamarckiana*. The absence of approximate flowering branches is against any relationship to *grandiflora*. The appearance of the small buds in the axils of the lower leaves is characteristic of some forms of *Oenothera biennis*. The pubescence of the stem is described by M. Gagnepain as very like the specimen of *grandiflora* and not at all like the specimen of De Vries's *Lamarckiana* sent for comparison.

2. INFLORESCENCE. The bracts of the inflorescence are not broad at the base and sessile as in the *Lamarckiana* of De Vries. They are narrow-elliptical and short-petioled.

3. BUDS. The size and form of the buds present perhaps the most important characters on the sheet. They are short and stout, and these characters alone make it impossible that the plant could have been *O. grandiflora* Solander. (Compare PLATE 38 with PLATE 37.) Forms of *O. biennis* frequently show these peculiarities. The sepals have a greater pubescence than those of *grandiflora*.

4. FLOWERS. The flowers are medium-sized, petals probably between 2 and 2.5 cm. long. They are not large enough for *grandiflora* or for the large-flowered forms of De Vries's *Lamarckiana*. The stigma (*s*, PLATE 38) appears to be at about the level of the anthers, the style not extending well beyond as in the types mentioned above. The flowers, in size and in the relation of the stigma to the anthers, agree with forms of *biennis*.

5. CAPSULES. The capsules appear to be of the *biennis* type, which is similar to that of De Vries's *Lamarckiana*.

In conclusion, the forms of the leaves and bracts distinguish this plant of Abbé Pourret from the *Lamarckiana* of De Vries's cultures. The size and form of the buds, the size of the flowers, and the position of the stigma distinguish it from *O. grandiflora* Solander as well as from the larger-flowered forms of De Vries's *Lamarckiana*. All of the characters described above are represented in the assemblage of forms included under the name *Oenothera biennis*. Since we know nothing of the rosette, general habit, and lower foliage of this plant, it is quite impossible to follow its determination further.

SHEET 3. SPECIMENS REFERRED BY DE VRIES TO *Oenothera grandiflora*

The specimens on this sheet (PLATE 39) are so imperfect and their form so abnormal that a satisfactory determination of their identity is probably impossible. De Vries (1901, footnote to p. 316) considered them to be *Oenothera grandiflora* Aiton = *O. grandiflora* Solander (*O. suaveolens* Desfontaines).

The sheet bears a label of Michaux with "Ameriq. sept." On this label in the handwriting of Desfontaines is "*Oenothera suaveolens* Hort. Paris." Above this name has been written "*Oenothera grandiflora* Poiret Encycl.," and below, Spach wrote "*Onagra vulgaris grandiflora* Spach." A second label bears the name "*Oenothera grandiflora*," probably in the handwriting of André Michaux. M. Gagnepain states that the specimens were imported as dried plants from North America. The chief interest in this sheet lies in the fact that Desfontaines evidently considered the specimens to be his own species *Oenothera suaveolens*.

Both specimens are entire plants, the smaller about 3.5 dm., the larger about 5 dm. in height. They are unbranched and obviously dwarfed. The leaves are petioled as in *grandiflora*, but those of the smaller plant are much below the average size for this species. The stigma (*s*, PLATE 39) shown in the flower of the smaller plant seems to be above the tips of the anthers as in *grandiflora*. The pubescence of the stems and sepals, from notes of M. Gagnepain, appears to be somewhat similar to *grandiflora;* it is not that of De Vries's *Lamarckiana*.

There appear to be no characters on these plants that might not have been those of *O. grandiflora* Solander under very unusual or abnormal conditions. There is, however, little or nothing in these specimens that is typical of *grandiflora*, and apparently nothing that determines a relationship to any other *Oenothera*. It is hardly possible that plants so different from one another grew together in the same environment and it seems more probable that they were quite unrelated. They remain to us as the flotsam of the herbarium, plants of whose precise origin and parentage we know nothing.

DISCUSSION

The reader will have noted that throughout this paper the name *Lamarckiana* has been kept strictly for the plant that has come down to us from the cultures of De Vries, a plant well known to scores of botanists and grown in numerous botanical gardens. If this paper has shown that Lamarck's plant in the gardens of Paris at about 1796 or earlier, the type of *Oenothera Lamarckiana* Seringe (1828), was a form of *Oenothera grandiflora* Solander (1789) the former name becomes a synonym of the latter. The *Oenothera*

of De Vries's cultures is left without a name or at least without the authority of Seringe. I propose, however, that the name "*Oenothera Lamarckiana* De Vries" be kept for this plant, which has been the subject of such extensive experimental study by De Vries and whose origin and behavior is a matter of such great interest to the geneticist.

The name when written "*Oenothera Lamarckiana* De Vries" is clear to all who have knowledge of the relation that this plant bears to the mutation theory. If there were evidence that "*O. Lamarckiana* De Vries" is or ever was a component of the American flora as a native species, there might be some reason to change its name. However, the evidence indicates that *Lamarckiana* has come to us greatly modified, that its parentage is far from pure, that it is in fact of hybrid origin. We are dealing with the product of the garden, and as such the plant may reasonably be exempt from a change of name that would carry endless confusion through the literature of experimental morphology. Should any taxonomist contemplate the introduction of a new name let him first ponder the inscription over the grave of William Shakespeare.

The introduction of *Oenothera grandiflora* Solander into England in 1778 marked a very important date in the development of the *Oenothera* flora over parts of Europe. This species undoubtedly holds the key to many puzzling herbarium sheets and records. Botanists do not yet realize how definite is our knowledge of this native American species and how clear is our information on its history. (See MacDougal, 1905, p. 7.)

Oenothera grandiflora Solander was discovered by William Bartram in 1776 near Tensaw, Alabama, on an expedition undertaken at the request of John Fothergill, M.D. Solander's original description in Aiton's Hortus Kewensis, 1789, from material grown at Kew, states that *O. grandiflora* was introduced by John Fothergill in 1778. A herbarium specimen in the British Museum from "Hort. Fothergill 1778" makes it evident that Bartram must have sent seed to Fothergill. The species still occupies its original station in Alabama, where it was rediscovered in 1904, and there is abundant herbarium material from this source; also, there are strains under cultivation by myself and others. As striking an American novelty as this large-flowered species would naturally be-

come widely distributed, which explains its presence in Paris somewhat earlier than ?1798, when Lamarck's description was published. Escaping from the gardens, the plant has been reported as growing wild at various stations in England and France. Following in the wake of its distribution to European botanical centers came the inevitable description as new species of forms derived from the original. *Oenothera suaveolens* Desfontaines and Lamarck's plant, *Oenothera Lamarckiana* Seringe, were undoubtedly such derivatives and must be considered as forms of *Oenothera grandiflora* Solander.

The identification of Lamarck's plant with *Oenothera grandiflora* Solander has very greatly modified the problem of the origin of "*Oenothera Lamarckiana* De Vries." The problem has become far more tangible. I have recently (Davis, 1911, p. 226, and 1912, p. 379) criticized adversely the evidence that has been offered to show that *Lamarckiana* was known previous to 1778 when *grandiflora* was introduced into England. With Lamarck's plant assigned to *grandiflora* we pass from the eighteenth century to periods when we may hope for more direct evidence than that furnished by the old accounts and figures.

We know that as a cultivated plant handled by seedsmen *O. Lamarckiana* first appeared about 1860, when it was placed on the market by the firm of Carter and Company of London, who state that their seed came from Texas. The identification by Lindley of these plants with *O. Lamarckiana* Seringe was undoubtedly incorrect. I have recently described and figured (Davis, 1912, p. 417) certain well preserved specimens of an *Oenothera* in the Gray Herbarium from a plant grown at Cambridge, Massachusetts, by Dr. Asa Gray in 1862. Evidence is there given which indicates that this plant held a close genetical relationship to these same cultures of Carter and Company, perhaps not more than one or two generations removed from the original plants. These specimens show characters in part those of De Vries's *Lamarckiana* and in part like *grandiflora*. If this plant grown by Dr. Gray was representative of the cultures of Carter and Company their plants must have differed from the *Lamarckiana* of today in a number of important particulars. I regard this herbarium sheet as the most important now known bearing on the problem of the origin of *Oenothera Lamarckiana*. Its relation to the writer's working hypothesis that

Lamarckiana arose as a hybrid between *biennis* and *grandiflora* has been fully discussed in the paper mentioned above.

Although Carter and Company state that they received their seed from Texas, it must be borne in mind that we have at present no confirmatory evidence that such a plant as they describe or as that represented on the sheet in the Gray Herbarium is native in the southern or southwestern United States. Here is a problem that well deserves the attention of botanists in these regions, who should make every effort to bring such a type to light that seed may be sent to the workers in the experimental gardens. If such a form grew in Texas no further back than 1860 it may surely be expected there today.

It is possible that the cultures of Carter and Company arose in England and that their association with a Texan source may have been some mistake on the part of the seedsmen. We have several accounts of large-flowered Oenotheras in England at dates previous to 1860. The most important and the earliest is that in Smith's English Botany (**22**: 1534. 1806) with the excellent figure of Sowerby. This account describes at this early date (1806) very extensive growths of an interesting form on the sand banks along the coast a few miles north of Liverpool. At the present day "*Oenothera Lamarckiana* De Vries" and variants from this type are established and flourishing over extensive tracts in the same region north of Liverpool through the sand hills of Lancashire. It is not impossible that the *Lamarckiana* of Carter and Company may have come from such regions.

The problem of the origin of "*Oenothera Lamarckiana* De Vries" must be approached from two sides. The English botanists have the problem of the history of such an *Oenothera* flora as that of the Lancashire sand hills, and collections should be searched with the greatest thoroughness for herbarium sheets that may be of assistance in tracing its development. American botanists have the problem of the discovery and isolation by cultures of the large-flowered Oenotheras throughout the south and west, which might have a direct relationship to *Lamarckiana* or which might be one of the parents of a possible hybrid. A good beginning was made in the rediscovery of *Oenothera grandiflora* Solander but the search should be pushed further.

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The effect of guanidin on plants*

OSWALD SCHREINER AND J. J. SKINNER

INTRODUCTION

Guanidin has been found in some plants. It may arise from the oxidation of arginin. Arginin is a decomposition product of proteins and exists in plants, and it has also been found in soils.† Interesting in this connection is the appearance of guanidin in seedlings, as reported by Schulze,‡ which probably results by further changes from arginin. Guanidin can also be formed by the oxidation of guanin in the laboratory.

Guanidin was shown to be toxic to plants, first by Kawakita § and later in this laboratory.‖ According to Shibata,¶ who studied the effect of *Aspergillus niger* on a number of nitrogenous compounds, this mold had no effect on guanidin. Hutchinson and Miller** include guanidin among the nitrogenous compounds assimilated by plants.

In the earlier experiments in this laboratory the guanidin carbonate was studied in various concentrations of distilled water. The wheat plants were killed in 9 days in solutions stronger than 100 parts per million. In all the lower concentrations, including 1 part per million, the wheat plants were seriously injured.

This harmful effect of guanidin has since then been more

* Contribution from the Laboratory of Soil Fertility Investigations, Bureau of Soils.

† Schreiner, O., and Shorey, E. C. The presence of arginin and histidin in soils. Jour. Biol. Chem. **8**: 381. 1910.

‡ Schulze, E. Ueber einige stickstoffhaltige Bestandtheile der Keimlinge von *Vicia sativa*. Zeit. Physiol. Chem. **17**: 193. 1893.

§ Kawakita, I. On the behavior of guanidin to plants. Bull. Col. Agr. Tokio **6**: 181. 1904–05.

‖ Schreiner, O., Reed, H. S., and Skinner, J. J. Certain organic constituents of soils in relation to soil fertility. U. S. Dept. Agr. Bur. Soils Bull. 47. 1907.

¶ Shibata, K. Über das Vorkommen von Amide spaltenden Enzymen bei Pilzen. Hofmeister's Beiträge **5**: 384. 1904.

** Hutchinson, H. B., and Miller, N. H. J. The direct assimilation of inorganic and organic forms of nitrogen by higher plants. Centralbl. Bakt. **30**: 513. 1911.

thoroughly studied, and in this later work nutrient culture solutions, 66 in number, have been used, comprising all the combinations of potash, phosphate, and nitrate, as explained below.

EXPERIMENTAL METHODS

Wheat seedlings were grown in aqueous culture solutions containing the ordinary fertilizer salts, calcium acid phosphate, sodium nitrate, and potassium sulphate. Some of the cultures contained calcium acid phosphate only, some sodium nitrate only, and some potassium sulphate only. Other solutions were composed of mixtures of two salts, sodium nitrate and calcium acid phosphate, sodium nitrate and potassium sulphate, and calcium acid phosphate and potassium sulphate. Still other solutions had all three constituents in various proportions. The concentration of all the solutions was 80 parts per million of the fertilizer ingredients, P_2O_5, NH_3, and K_2O. In cultures containing only one fertilizer salt, for instance calcium acid phosphate, the concentration was 80 parts per million of P_2O_5. If two salts were present, for instance calcium acid phosphate and sodium nitrate, the concentration was 80 parts per million of $P_2O_5 + NH_3$. If all three salts were present, the concentration was 80 parts per million of $P_2O_5 + NH_3 + K_2O$. The ratios of the constituents varied in 10 per cent stages. In all, there were 66 different cultures of nutrient solutions.

For a more detailed explanation of this triangular scheme and the principles involved in preparing culture solutions in definite progression of its constituents, the reader is referred to earlier publications.*

Two sets of cultures were prepared; to one set was added merely the nutrient salts, while to each culture of a similar set guanidin carbonate was added in amounts of 25 parts per million in addition to the nutrient salts. The culture solutions were contained in wide-mouth bottles, holding 250 c.c., and 10 wheat seedlings grown in each culture. The culture solutions were changed every three days, four changes being made in the course of the

* Schreiner, O., and Skinner, J. J. Some effects of a harmful organic soil constituent. U. S. Dept. Agr. Bur. Soils Bull. 70. 1910. Ratio of phosphate, nitrate and potassium on absorption and growth. Bot. Gaz. **50**: 1. 1910.

experiment. The solutions were analyzed for nitrates immediately after each change. The phosphate and potassium were determined on a composite solution of the four changes. Observations on the general development of the plants and the effect on root growth and appearance were made during the experiment, and photographs were taken.

For the purpose of preparing the 66 culture solutions needed in this investigation, stock solutions of the three salts, calcium acid phosphate, sodium nitrate, and potassium sulphate, were prepared separately. The salts were chemically pure salts and were dissolved in each case in physiologically pure water. For the calcium acid phosphate solution 1.776 grams of $CaH_4(PO_4)_2 \cdot H_2O$ per liter were used. This solution has a concentration of 1,000 parts per million of P_2O_5. The sodium nitrate solution was prepared by using 5,000 grams of $NaNO_3$ per liter. This solution is equivalent to a concentration of 1,000 parts per million of NH_3. The potassium sulphate solution was prepared by dissolving 1.852 grams of K_2SO_4 per liter. This solution has a concentration of 1,000 parts per million of K_2O. The amount of culture solution used in each culture bottle being 250 c.c., it follows that every 2 c.c. of these 1,000 parts per million stock solutions will represent 8 parts per million in the culture solution when this is diluted to the capacity of the bottle; i. e. the successive addition of 2 c.c. of the stock solution gives the 10 per cent differences desired in putting up the 66 solutions. In putting up the 66 cultures it was found desirable to calibrate each bottle for 250 c.c. capacity and to number them consecutively from 1 to 66. Bottles in which the 250 c.c. mark was either high or low were discarded, only those being used that brought the surface of the liquid from one-half to one centimeter from the top. These 66 bottles were then arranged in a triangular form, as illustrated by FIG. 1 and 2.

The necessary amount of the 1,000 parts per million stock solution above described was measured from a burette. For instance, in adding the requisite amount of nitrate to the set of culture bottles the line of bottles P to K in FIG. 2 received no nitrate solution, the next line of bottles received 2 c.c. each, the third line 4 c.c. each, and so on, increasing 2 c.c. with each successive line, the culture at N receiving 20 c.c. of the nitrate solution.

Likewise, in adding the requisite amount of potash, the cultures in the line P to N received none, the cultures in the next line received 2 c.c. each, in the third line 4 c.c. each, and so on up to the culture at K, which received 20 c.c. of the potash solution. The phosphate solution is added in the same manner, none to cultures in line K to N, 2 c.c. to cultures in the second line, and so on up to the culture at P, which received 20 c.c.

Each bottle received, therefore, a total of 20 c.c. of one, two, or three of the stock solutions, depending upon whether it was at the apex, along the sides, or in the interior of the triangle. All of the cultures were then diluted up to the 250 c.c. mark.

In this investigation, as already mentioned, the culture solution contained 25 parts per million of the guanidin carbonate. The amount of this carbonate to be added to each culture bottle of 250 c.c. was, therefore, 6.25 milligrams. Of the 250 c.c., 20 c.c. were already contained in the bottles in the form of the fertilizer salt solution. Therefore the solution with which the fertilizer salt solution in the bottles was to be diluted consisted of 6.25 milligrams of the compound dissolved in 230 c.c. of pure water or 27.17 milligrams per liter. A sufficient quantity of this strength of solution was prepared to fill the 66 bottles.

As a means of comparing the cultures grown in these solutions containing the guanidin, it was necessary to put up cultures prepared in exactly the same way, except that pure water was used.

In all of this work physiologically pure water was used. This was prepared by shaking ordinary distilled water with a highly absorptive carbon black, as described in earlier publications,* which removes from the water any injurious property it may possess.

The culture solutions were now ready to receive the plants, which were thereafter grown in a greenhouse under suitable conditions.

In this work it was necessary to have a large number, often several hundred, and sometimes thousands of uniform seedlings, i. e. seedlings of the same age and equal development and general vitality.

The manner of growing the seedlings and the method of inserting them in the above culture solutions were as follows:

* Livingston, B. E., et al. Further studies on the properties of unproductive soils. U. S. Dept. Agr. Bur. Soils Bull. 36. 1907.

Perforated aluminum disks were floated, by means of a raft prepared from sealed glass tubing, in such a way that the disks were kept just at the surface of the water when loaded with seeds.

The wheat seeds, previously soaked in water, for about two hours, not longer, were spread evenly on the surface of the disks. The perforations in the 1.6 mm. thick aluminum were approximately 3.2 mm. in diameter and 2 mm. apart. The entire arrangement of raft and disks was floated in a porcelain-lined iron tank. The seedlings were used when the plumule was about 2 cm. high and just ready to emerge from the enveloping sheath. In this manner the 1,320 uniform seedlings required for each experiment were readily obtainable.

The bottles used in these cultures were made of flint glass and were stoppered by means of a soft flat cork about 12 mm. in thickness and notched for holding the seedlings. The method of notching these corks consisted in cutting 10 vertical, triangular wedges from the circumference of each. Each wedge after being cut out was truncated, so that when it was replaced, a small triangular opening was left through which the plumule of the seedling passed. This hole was large enough to hold the seedling firmly and yet not bruise or injure it in any way by pressure. Around the circumference of the cork, in the upper half, a groove had been made sufficiently large to hold a small rubber band. After the wedges were inserted, the band kept them in place and allowed the cork with the seedlings to be handled readily and put into or taken out of the bottle without disturbing the plants.

As already mentioned, these solutions were changed every three days. This was done by putting up other triangles of bottles similar in every respect to the ones just described. The corks with the plants were then transferred from the old solution to the corresponding new solution.

EFFECT OF GUANIDIN ON WHEAT

As already mentioned, two sets of the cultures were prepared; one was used as a control; to the other was added guanidin carbonate, 25 parts per million to each culture. The wheat seedlings grew from February 15 to February 27, 1911, the solutions being changed every three days.

For the first few days no difference was noticeable between the control and the guanidin set. About the fifth day bleached spots appeared in the leaves in some of the cultures, producing an effect like a plant disease. The diseased spots on the leaves spread and became larger and more numerous. The spots appeared first on a few cultures, but when the cultures were arranged in the order of their composition the reason for this became evident. The guanidin effect showed itself first in the cultures high in nitrate and then spread to those lower in nitrate, until the series of no nitrate content was reached. In this series the guanidin effect was scarcely discernible. As the plants grew older, the guanidin effect became more and more marked; the bleached spots

FIG. 1. Effect of guanidin on wheat plants; series *A* without guanidin, series *B* with guanidin.

coalesced and appeared most marked in the lower part of the leaves; the leaves broke finally, presenting on the whole an effect similar to that produced by a wilt disease and accompanied with considerable bleaching of the green parts of the plant. This, at least, was the effect in all of the cultures containing nitrate and was the more marked the higher the nitrate content. The series containing no nitrate whatever retained its green color and was not subject to collapse or wilting, although here and there some bleached spots appeared.

In FIG. 1 are shown the two sets of cultures. *A* is the normal or control set and *B* the guanidin set. The distinctly destructive effect of the guanidin is apparent in the blighted appearance of set *B* in striking contrast to the fine growth in the control cultures, which is even more marked than the photograph can show because of the deep green color of the normal set contrasted with the bleached appearance of the guanidin set.

FIG. 2. Effect of guanidin on wheat plants. Nearer view of series *B* in FIG. 1.

In FIG. 2 a nearer and better view is had of this guanidin set. The plants are arranged according to the composition of their culture solutions, thus forming a triangle. By this arrangement the highest nitrate culture appears at *N*, the highest phosphate culture at *P*, and the highest potash culture at *K*. It is apparent that the poorest plant development occurs in those cultures high in nitrate but is distinctly noticeable in every culture except in the line of cultures from *P* to *K*, which is the series containing no nitrate. The plants in this line of cultures are firm and erect, as can be seen in the photograph. In actuality this difference is accentuated by the nearly normal green color of this series, whereas

all other cultures, in addition to the dilapidated condition, had a decidedly bleached appearance.

The effect of the nitrate in increasing the harmful effect of guanidin is also shown by the weight of the tops taken at the termination of the experiment. In TABLE I the first column gives

TABLE I

EFFECT OF GUANIDIN ON GROWTH AS INFLUENCED BY NITRATE

Culture series	NH_3 as nitrate in fertilizer mixture, parts per million	Green weight of cultures, grams		Relative growth. Control = 100
		Without guanidin	With 25 parts per million guanidin	
66	80	1.656	0.520	31
55–65	72	4.178	1.990	47
45–64	64	6.860	3.412	48
36–63	56	9.449	5.031	53
28–62	48	12.359	6.874	55
21–61	40	15.998	8.394	52
15–60	32	18.649	11.491	62
10–59	24	21.691	13.602	62
6–58	16	23.327	15.709	67
3–57	8	20.923	17.288	83
1–56	0	16.156	15.195	94

the series, the cultures of which have like nitrate content. The amounts of nitrate in each culture of these series are given in the second column. The third and fourth columns give the weight of the tops of the plants grown in the cultures without and with 25 parts per million of guanidin carbonate. It is at once apparent that the guanidin is very harmful to growth. The total green weight of the 66 cultures in the normal set was 151.2 grams against only 99.5 grams in the guanidin set. Placing the normal at 100, the growth in the guanidin set becomes 66. The last column gives the relative growth in each of the series of uniform nitrate content in the set. The culture that contained 80 parts per million NH_3 as nitrate gave a relative weight of only 31 or a decrease in growth of 69 per cent, whereas in the series of cultures that contained no nitrate the relative growth was 94, a decrease of only 6 per cent below the control. As shown in the table, the relative weight of tops obtained increased with decreasing nitrate content.

The effect of guanidin on growth, and especially the harmful influence of the nitrate, was considered so remarkable, particularly

in the light of the previously observed beneficial effect of nitrate in conjunction with harmful compounds,* that the entire experiment was repeated, and it gave absolutely the same results.

The plants grew from March 17 to March 29. Again the effect of the guanidin did not appear until about five days had elapsed, and again it showed itself first, and later most marked, in the high nitrate solutions. Again the no nitrate cultures were left practically unharmed. The total green weight for the normal set was 163.9 grams, and in the guanidin set it was 116.3 grams, a relative green weight of 71. The weights of the tops in the different nitrate series are given in TABLE II, the arrangement being

TABLE II

EFFECT OF GUANIDIN ON GROWTH AS INFLUENCED BY NITRATE

Culture series	NH_3 as nitrate in fertilizer mixture, parts per million	Green weight of cultures, grams		Relative growth. Control = 100
		Without guanidin	With guanidin	
66	80	2.201	1.003	46
55–65	72	4.040	2.040	50
45–64	64	7.275	4.021	55
36–63	56	10.359	5.996	57
28–62	48	13.387	7.544	56
21–61	40	17.394	10.110	58
15–60	32	20.821	13.204	63
10–59	24	22.769	16.952	74
6–58	16	25.614	18.141	71
3–57	8	24.097	21.112	81
1–56	0	15.969	16.164	100

exactly the same as in TABLE I. The last column, giving the relative green weight of the different nitrate series, again shows the greater harmfulness of the guanidin in the series containing nitrate, which is especially marked in those high in nitrate.

In the first experiment the solutions were also analyzed for phosphate, nitrate, and potash. The results show a marked decrease in the absorption of the nutrient salts on the part of the guanidin plants, although the roots themselves were not noticeably affected, as is apparent from the plants visible in FIG. 1 and 2.

The total phosphate, nitrate, and potash removed by the normal plants was 1,608.9 milligrams, against only 1,088.5 milli-

* Schreiner, O., and Reed, H. S. The power of sodium nitrate and calcium carbonate to decrease toxicity in conjunction with plants growing in solution cultures. Jour. Amer. Chem. Soc. **30**: 185. 1908.—Schreiner, O., and Skinner, J. J. Some effects of a harmful organic soil constituent. Bot. Gaz. **50**: 161. 1910.

grams in the guanidin set. The phosphate removed was 427.3 milligrams in the control and 287.0 milligrams in the guanidin set; the potash was 723.7 milligrams for the control and 496.7 milligrams for the guanidin set; the nitrate was 457.9 milligrams for the control cultures and 304.8 milligrams for the guanidin cultures.

Tests of guanidin carbonate in quantities of 50 parts per million were also made in soil cultures. The physiological effect of the guanidin was again apparent in the spotting and bleaching of the leaves and was again most evident in the soils fertilized with nitrate.

EFFECT OF GUANIDIN ON OTHER PLANTS

The effect of guanidin was further studied by using plants other than wheat. In FIG. 3 is shown its effect on corn growing

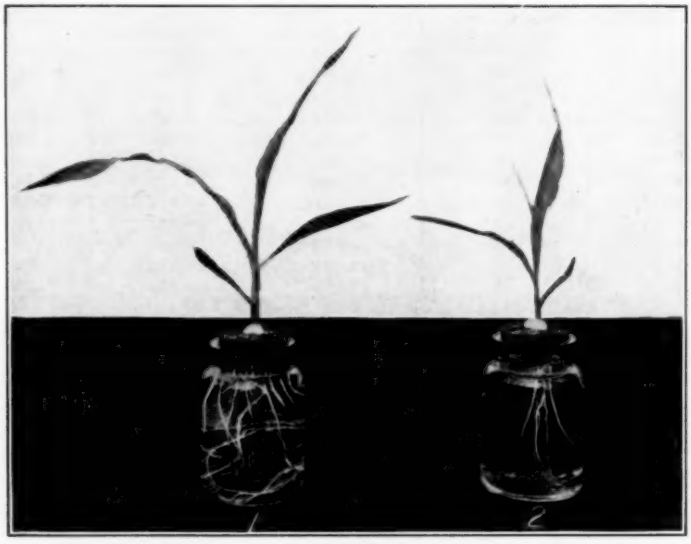

FIG. 3. Harmful effect of guanidin on corn; no. 1 without guanidin, no. 2 with guanidin.

in culture solution no. 41, containing 16 parts per million phosphate, 32 parts per million nitrate, and 32 parts per million potash. FIG. 4 shows the effect of guanidin on cowpeas, the control and guanidin cultures being in duplicate. FIG. 5 shows its effect on the potato plant. In these tests guanidin was used in concentra-

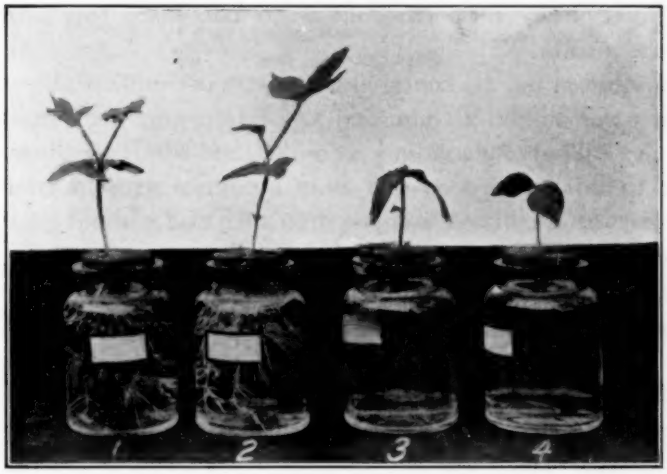

FIG. 4. Harmful effect of guanidin on cowpeas; no. 1 and 2 without guanidin, no. 3 and 4 with guanidin.

tions of 25 parts per million. With all these plants the harmful effect on growth is clearly shown and the same general physiological action was manifested as in the case of wheat.

FIG. 5. Harmful effect of guanidin on potatoes; no. 1 without guanidin, no. 2 with guanidin.

INFLUENCE OF ORGANIC NITROGENOUS COMPOUNDS

In regard to the influence of nitrate in increasing the harmfulness of guanidin some further studies were made which indicate

that other nitrogenous compounds do not share this property with the nitrate.

To solution no. 41, containing 16 parts per million phosphate, 32 parts per million nitrate, and 32 parts per million potash, 25 parts per million of guanidin were added, and wheat seedlings were grown in this solution as well as in a control without guanidin. A similar set of cultures was prepared with and without guanidin, but with this difference that the nitrate was omitted entirely and an equivalent amount of nitrogen in the form of asparagin was added to the culture solution. The plants grew from March 10 to March 23, 1911.

The characteristic effects of guanidin were noticed in the culture containing nitrate but did not appear in the culture containing asparagin. The appearance of the cultures is shown in

FIG. 6. Effect of guanidin with nitrogen in different forms; no. 1, nutrient solution containing sodium nitrate; no. 2, same plus guanidin; no. 3, nutrient solution containing asparagin; no. 4, same plus guanidin.

FIG. 6, where no. 1 is the control with nitrate and no. 3 the control with asparagin. No. 2 and 4 are the guanidin cultures to be compared with each other and with their respective controls. No. 2 shows the wilting effect of the guanidin as well as the decreased growth. The colors of the various cultures brought out the difference even more strikingly. The green weights given in TABLE III bear out the same point.

TABLE III

EFFECT OF GUANIDIN IN CULTURE SOLUTIONS CONTAINING NITROGEN AS NITRATE AND AS ASPARAGIN

Culture solution	Green weight, grams
$CaH_4(PO_4)_2$, $NaNO_3$, K_2SO_4	4.0
$CaH_4(PO_4)_2$, $NaNO_3$ + 25 parts per million guanidin, K_2SO_4	2.5
$CaH_4(PO_4)_2$, Asparagin, K_2SO_4	3.5
$CaH_4(PO_4)_2$, Asparagin + 25 parts per million guanidin, K_2SO_4	3.3

Creatinin was also tried in this same manner. Creatinin was identified as a soil constituent in this laboratory* and also found to be a constituent in a number of plants.† Its effect on plants has been shown to be beneficial, its action being to replace nitrate in producing plant growth.‡ The results obtained by using creatinin as the source of nitrogen instead of sodium nitrate in conjunction with the guanidin are given in TABLE IV.

TABLE IV

EFFECT OF GUANIDIN IN CULTURES CONTAINING NITROGEN AS NITRATE AND AS CREATININ

Culture solution	Green weight, grams
$CaH_4(PO_4)_2$, $NaNO_3$, K_2SO_4	3.4
$CaH_4(PO_4)_2$, $NaNO_3$ + 25 parts per million guanidin, K_2SO_4	2.4
$CaH_4(PO_4)_2$, Creatinin, K_2SO_4	3.0
$CaH_4(PO_4)_2$, Creatinin + 25 parts per million guanidin, K_2SO_4	3.0

* Shorey, E. C. The isolation of creatinin from soils. Jour. Amer. Chem. Soc. **34**: 99. 1912.

† Sullivan, M. X. The origin of creatinin in soils. Jour. Amer. Chem. Soc. **33**: 2035. 1911.

‡ Skinner, J. J. The beneficial effect of creatinin and creatin on growth. Bot. Gaz. **54**: 152–163. *f.* 1. 16 Au 1912.

Again the characteristic effect of the guanidin was observed in the cultures containing nitrate, and the depressed growth is shown by the green weight in the table. With creatinin the effect of guanidin was not apparent either in appearance or in the green weight obtained.

SUMMARY

Guanidin, as carbonate, is shown to be harmful to wheat, corn, cowpeas, and potato plants. It produces an effect similar to a physiological disease. The plant is normal for a few days, then begins to show a spotted appearance on leaf and stem. This effect develops until the plant is bleached to a considerable extent, with final collapse.

This harmful effect of guanidin on plants is augmented by the presence of nitrate and increases with the amount of nitrate present.

Sources of nitrogen, other than nitrate, did not show this same effect. The organic nitrogenous compound asparagin, as well as the beneficial soil constituent creatinin, appeared in fact to be able to counteract the effect of guanidin itself.

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WASHINGTON, D. C.

Polycodium

C. B. Robinson

The statements by which Professor E. L. Greene* suggested the resuscitation of Rafinesque's name require quotation in full, as they bring up many points open to controversy.

"We have in the Eastern and Southern United States two groups of vacciniaceous shrubs either of which is at variance with all genuine *Vaccinium* in two important points of floral structure. The corollas in both groups are campanulate, while in both *Vaccinium* and *Gaylussacia* they are urceolate. The stamens also, in these campanulate-flowered shrubs, are of a structure so peculiar that, on the characters of this organ alone, a genus might reasonably be established, were concomitant characters wanting. *Vaccinium* and *Gaylussacia* are now everywhere admitted as distinct, yet, exclusive of the groups here under special notice, there is not the slightest difference of floral structure between the two. But these other shrubs depart widely from the characters of both *Vaccinium* and *Gaylussacia* not only in their open-campanulate corollas, but in respect to their stamens, which organs are doubly marked by extremely long and slender anther-tubes, and two prominent horn-like projections on the back; so that nothing approaching these characters is found in any other genera allied to *Vaccinium*.

"Twice in the early part of the century, botanists of first-class ability proposed the separation of these species from *Vaccinium*. Rafinesque in 1818, not distinguishing generic differences between those types represented by *V. stamineum* and *V. arboreum* respectively—perhaps not even knowing *V. arboreum*—proposed the *V. stamineum* group for a genus under the beautifully appropriate name of Polycodium; and Nuttall in 1843, ignoring Rafinesque's earlier proposition—just as later pretenders to taxonomic autocracy suppressed Nuttall's work—sought to establish a new genus *Batodendron* with *V. arboreum* as typical, and *Picrococcus* with *V. stamineum* for its type.

"The characters of the two genera are well indicated by Nuttall, in the transactions of the American Philosophical Society, with the exception of one new and most significant peculiarity of the *V. stamineum* group which I alone seem to have observed.

* Pittonia 3: 323. 1898.

It is this, that in this group the corollas are *open in the bud!* For from ten days to two weeks before the actual flowering, and even from the time that the buds are green and scarcely larger than a pin-head, the corolla is open and campanulate. This is another character otherwise unknown in the family of plants to which these belong. Certainly in *Vaccinium* and *Gaylussacia* the buds are tightly closed, in an imbricate aestivation, until the corollas are full-grown and the anthers mature."

Now of vacciniaceous plants found within the limits of the United States, the genera that are almost universally recognized are *Chiogenes*, *Gaylussacia*, and *Vaccinium*. Even regarding these there is some controversy. *Chiogenes* is readily distinguished by the position of the ovary, only slightly inferior in flower, distinctly inferior in fruit, and while American and British authors of recent years have agreed in placing it near *Vaccinium*, German authors on the other hand believe the closest affinity to be *Gaultheria;* and it can hardly be denied that its position is somewhat intermediate,

There is no doubt as to the identity of *Gaylussacia*, as it was published as monotypic, its type, *G. buxifolia* H. B. K., agreeing with many species now known from South America, in the possession of evergreen leaves and non-succulent fruit as well as of a 10-celled ovary. The only species described as a *Gaylussacia* from Mexico or Central America does not belong to the genus, all of the species so called in the United States have succulent fruit, and all but one have deciduous leaves. Niedenzu* has placed that one in the Vitis-Idaea section of *Vaccinium*, and the other North American species in the Cyanococcus section of *Vaccinium*, retaining the name *Gaylussacia* for South American species only.

Kuntze,† also, has taken up the name *Adnaria* Raf.‡ for *Gaylussacia*, but the most positive thing that can be said about Robin's description,§ upon which Rafinesque's was based, is that it does not agree with that of any species of the family found in America and in particular disagrees with *Gaylussacia* in the very character relied on for its differentiation, the number of cells in the ovary.

* Engl. Bot. Jahrb. **11**: 193. 1889.

† Rev. Gen. Pl. 382. 1891.

‡ Fl. Ludov. 56. 1817.

§ Voy. Int. Louisiana **3**: 422. 1807.

Yet, taken on a summary of characters, there is probably no species found in Louisiana that is more likely to have been the basis for Robin's description than *Gaylussacia dumosa* (Andr.) A. Gray.

All of the remaining species of the family found north of the Mexican border are retained by many authors in *Vaccinium*. Generic or sectional segregation has been proposed on several characters, taken singly or in combination, the degree of union of the corolla, its aestivation, its shape, the presence or absence of awns on the anthers, the presence or absence of pubescence on the filaments, the presence or absence of false partitions in the ovary, the nature of the inflorescence, and tetramerous as contrasted with pentamerous flowers.

In the Thibaudieae, the other subfamily of Vacciniaceae, general agreement has been reached that the primary basis of differentiation should be sought in the stamens. There is much reason to believe that this is equally true with regard to the *Vaccinium* group, but it would be useless to belittle the fact that the weight of botanical opinion has been otherwise. The most popular segregate has been *Oxycoccus*, from which *Hugeria* has further been discriminated. They differ from the remainder of the group and from one another in the degree of division of the corolla. Possibly *Polycodium* will prove the most acceptable of the others. But on what grounds should it be retained? Professor Greene's claims for it are excessive, although indefinite, for he does not define "genuine *Vaccinium*." It has a campanulate corolla: so have *V. arboreum* Marsh.,* *V. Vitis-Idaea* L., *V. poasanum* Donn. Sm., *V. confertum* H. B. K., and others, differing from one another in various characters, and none except the first closely allied to *Polycodium*. The 10 stamens of *Polycodium* have pubescent filaments and 2-awned anthers: except in number they differ from the great majority of species of the eastern and southern United States, which have pubescent filaments but awnless anthers (section Cyanococcus), from most of those of the western States, which have 2-awned anthers but glabrous filaments (section Euvaccinium), but agree with many tropical American species,

* No opinion is necessarily expressed in giving the name of this or any other species as *Vaccinium*.

such as *V. leucanthum* Schlecht., *V. stenophyllum* Steud., and *V. cubense* Griseb., none at all closely allied to *Polycodium*. This is not all, for in the United States no single character is as certain to ensure the instant identification of *Polycodium* as the long-exserted anthers; moreover, the tubes forming the prolongation of the anther cells are unusually long, both absolutely and relatively to the anther cells. But there is a Mexican species, *Vaccinium Kunthianum* Klotzsch, so closely related to *Polycodium stamineum* that neither Kunth nor Dunal* thought it worthy of specific rank. Its stamens were described as half-exserted, and figured as well exserted, but in no collection that I have seen, so identified by others or by myself, can they be considered as more than barely exserted, the anthers are shorter than in the other species, and the anther tubes only about one and a half times the length of the anther cells. In all other respects it is a perfectly good *Polycodium*, and if the genus is to be maintained, must be transferred to it, forming a section by itself, on the basis of the characters just stated.

Finally, the anther awns are often revolute, but too much emphasis should not be placed on this, as it is not always constant within a single flower; at least, however, they are divaricate, but so they are in species which no one has suggested separating from *Vaccinium*, such as *V. caespitosum* Michx.

The flowers of *Polycodium* are articulated with the pedicel; this is also true of certain species placed in *Vaccinium* by most authors, notably of the *Disterigma* species. That group, which does not come north of Mexico, was until recently treated by all authors as a section of *Vaccinium*, but Niedenzu† and Hörold‡ so far separate it from that genus that they place it in the Thibaudieae. On the basis of floral characters there seems to be no reason for so wide separation; indeed, unless *Vaccinium* is to be radically divided, I at least believe that there is as much reason for placing *V. Myrtillus* L. and its American allies in a different genus from *V. corymbosum* L. and its allies, as there is for so segregating *Disterigma* from the latter. Drude§ has placed considerable

* H. B. K. Nov. Gen. & Sp. **3**: 267. *pl. 253.* 1819; DC. Prodr. **7**: 568. 1839.

† Engl. Bot. Jahrb. **11**: 209. 1889.

‡ Engl. Bot. Jahrb. **42**: 282. 1909.

§ Engler & Prantl, Die Nat. Pflanzenfam. 4^1: 32. 1889.

emphasis on articulated pedicels as a means of distinguishing the Thibaudieae from the Vaccinieae but, unfortunately, has gone far beyond the facts.

One character remains to which Professor Greene has called particular attention, the open aestivation of the corolla. All evidence that has been obtained confirms his statement on this point for every species of *Polycodium*, including *V. Kunthianum*. This does seem of such importance that the genus may properly be maintained; the other characters previously mentioned may be treated as collateral, by one who is dealing with the species of America north of Mexico, but it must be remembered that not one of them can be relied on to distinguish *Polycodium* from all other genera, even within the limits of North America.

Rafinesque* published *Polycodium* thus: "67. The species of *Vaccinium* with campanulated corollas, must form a peculiar genus or subgenus, *Polycodium*. In fact the whole tribe of *Ericacea* or *Bicornia* must be newly modelled." And this is all, with one very important exception. The paragraph occurs in a review of Pursh's Flora Americae Septentrionalis and may fairly be interpreted by reference to that work. Pursh divided *Vaccinium*† primarily into species with deciduous leaves and those with evergreen leaves, dividing each of these in turn on the basis of campanulate as contrasted with urceolate corollas. His species with deciduous leaves and campanulate corollas were *V. stamineum*, *V. album*, *V. arboreum*, *V. dumosum*, *V. frondosum*, and *V. pallidum;* those with persistent leaves and campanulate corollas were *V. Vitis-Idaea*, *V. myrtifolium*, and *V. crassifolium*. *Vaccinium stamineum* thus comes first, and *V. album* Pursh is regarded by most authors as the same species. *Polycodium*, therefore, may be held to be typified by *Vaccinium stamineum* L., but Rafinesque's genus in its entirety was a mixture of widely differing elements, including representatives not only of *Batodendron* but of *Gaylussacia* and of different sections still included in *Vaccinium* by nearly all authors.

Picrococcus of Nuttall is based almost entirely on *Vaccinium stamineum* L. (including *V. elevatum* Banks & Soland.) with the

* Am. Monthly Mag. 2: 266. 1818.

† Fl. Am. Sept. 1: 284–290. 1814.

addition of a second species, *Picrococcus floridanus*, certainly congeneric with the former, of which more hereafter.

Professor Greene is unduly critical of Nuttall for overlooking or disregarding such a publication as Rafinesque's of *Polycodium* for the genus containing *Vaccinium stamineum*, and Nuttall was not the first offender. In 1836 Rafinesque himself has the following:* "ADNARIA Raf. fl. lud. probably a subgenus of the *Codorolla* or Vacciniums with bell flowers, which see." But *Codorolla* does not appear again, and Rafinesque did not consider this reference worth indexing.

It is apparent that the adoption of *Polycodium* as a generic name, to be typified by *Vaccinium stamineum* L., is barely justified.

Before leaving the subject of generic subdivision in the *Vaccinium* alliance it is desired to amplify a statement above made with regard to the importance of characters derived from the stamens. The anthers may be 2-awned or awnless. In a solitary specimen, *Wright 2202*, referred to *Vaccinium Ramonii* Griseb., some anthers were found with a single central awn. Further examination showed that this was not a constant character, even within a single flower; but none of the anthers were awnless. The value of anther awns as a diagnostic character obviously depends upon the degree of their constancy, and final judgment will be influenced, consciously or unconsciously, by the nature of the grouping thus achieved.

Examination of the flowers of every species but one, found within the limits of North America, as well as of some extralimital material, gives this result. There are 3, or more likely only 2, species, *V. meridionale* Sw., of Jamaica, *V. consanguineum* Klotzsch, of Panama and Costa Rica, and *V. multiflorum* Benth., of Colombia, in which this character has to be handled with extreme caution. All of these are very closely allied; indeed, it is doubtful if the first two can be held distinct. In all of these the awns are very delicate and often closely appressed, to such an extent that they might escape detection, unless considerable care be taken in their search. Further, in *V. meridionale* they are often so reduced that they are practically wanting, yet other stamens in the same flower may possess them, slender and short

* New Fl. 1: 65. 1836.

indeed, but certainly present. Moreover, *V. multiflorum* was described as having anthers alternately awned and awnless, yet a recent collection from near its type locality, *Pittier 1182*, agreeing otherwise with Bentham's description, has all the anthers of such flowers as were examined 2-awned, with awns as described and found for this and for *V. consanguineum*. The plate* of *V. meridionale* is wrong in this respect.

Yet, all these can be described as awned anthers, and on other grounds the alliance of the species is with those possessing awned anthers. Much search has failed to disclose a single other exception, not only within the limits of a species but within the limits of what appear to be groups of related species.

It may be added that the presence of pubescence, in whatever degree, on the filaments or the connectives—and when it occurs it is usually on both—is equally conclusive but of secondary importance. Thus, if a vacciniaceous plant be found in America north of Mexico with awnless anthers and glabrous filaments, no further information is needed for its determination as *Gaylussacia frondosa* (L.) T. & G., except by those who consider *G. nana* (A. Gray) Small and *G. tomentosa* (Pursh) Chapm. to be specifically distinct from that speci[illegible] Each of the other three combinations of these two characters will describe large groups of species.

On the other hand, investigation of the relative length and degree of divergence of the awns and of the relative amount of pubescence on the filaments seems to indicate that these do not afford reliable characters except possibly in rare cases.

Up to the present the following have been ascribed to *Polycodium* as distinct species: *P. caesium* Greene, *P. candicans* (C. Mohr) Small, *P. elevatum* (Banks) Greene, *P. floridanum* (Nutt.) Greene, *P. Langloisii* Greene, *P. melanocarpum* (C. Mohr) Small, *P. neglectum* Small, *P. oblongum* Greene, *P. oliganthum* Greene, *P. revolutum* Greene, and *P. stamineum* (L.) Greene; it has already been stated that another species awaits transfer, *Vaccinium Kunthianum* Klotzsch. The last having been separated on the basis of its shorter anthers, not or barely exserted, the character depended on as of next importance is the relation between leaves or bracts and the inflorescence.

* Sw. Ic. Ind. Occ. *pl. 12.* 1794.

In the *Vaccinium* group as a whole there is a transition in this respect, and *Polycodium* is merely one case of many. In certain species, such as *V. caespitosum* Michx., *V. scoparium* Rydb., and *V. Myrtillus* L., the flowers are few in number on a branch borne in the axils of what are apparently quite normal leaves as to size, shape, and texture. In others the inflorescence is quite clearly racemose, or by contraction fasciculate, the pedicels subtended by bracteoles quite different in appearance from the vegetative leaves. This includes nearly all the species of the eastern United States. There is yet a third group, which almost perfectly links the two, the inflorescence being perhaps best described as a leafy raceme. These are mostly tropical plants. Incidentally, these three groups follow rather closely the lines indicated by the stamens.

In the case of *Polycodium* there is a group "in which," to use Nuttall's expression* when describing *Pricrococcus floridanus*, "the flowers appear truly axillar." Here also belong the names *Polycodium caesium* Greene, *P. oliganthum* Greene, and *P. revolutum* Greene. Nuttall's type seems to have perished, which will cause trouble to those who believe this group to contain more than one species, for he has no sufficient description for more definite determination. In the case of the other species duplicates of the type collections have been examined, and there seems no sufficient reason for holding them distinct. In separating *P. revolutum* from *P. caesium* Professor Greene† relies chiefly on the leaves of the former being more pubescent, more oval and obtuse, their margins revolute, the calyx lobes deeper, acute or acuminate instead of scarcely acute, and deeper corolla lobes. It is not possible to separate the series of specimens on these characters or any of them, those drawn from the leaves being especially unreliable, not even holding for the collections on which the species were based. There seems even less reason for segregating *P. oliganthum*.

Now, the same thing happens in *Polycodium* as in the *Vaccinium* group in general; the leaves, in the axils of which the flowers are borne, are often reduced in size but still retain the other characters of the typical leaves of the plant; yet again, they may

* Trans. Am. Philos. Soc. II. **8**: 262. 1843.

† Pittonia **3**: 249, 250. 1897.

be very greatly reduced although sometimes differing considerably within the same inflorescence. *P. oliganthum* approaches the former condition but seems to have been referred correctly to the *P. floridanum* group. The linking material affords some justification for the view that specific lines should not be drawn on this character, but the corolla in the group thus separated is always smaller, one half to one third of the length of that of the remaining species, and it seems preferable to consider it as distinct and as forming a single species only. Its range is from South Carolina to Florida, all of the types of the species proposed having come from the latter state. If this view be accepted, there seems no reason why its name should not be *Polycodium floridanum* (Nutt.) Greene.

From the remainder it is exceedingly easy to separate *Polycodium neglectum* Small by means of its glabrous branchlets and leaves. These characters hold definitely for large series of collections, but there seem no others correlated with them, and the plants often grow side by side with those of *P. stamineum*. It is, therefore, a matter of opinion as to whether the two should be held distinct.

Polycodium melanocarpum was described by Mohr* as *Vaccinium stamineum melanocarpum* without a definite type specified. It was raised to specific rank by Kearney,† who expressly stated that his own collections were not typical. Mohr,‡ subsequently discussing it as a species, gives as the type locality "Mountain region of Alabama. More specifically, St. Clair County, near Ashville, July 1880." The ground for separation was the succulent nature of the fruit and its color. Mohr also proposed two varieties, *V. melanocarpum candicans* and *V. melanocarpum sericeum*. In Small's Flora§ the former variety becomes *P. candicans* (C. Mohr) Small, and *Polycodium melanocarpum* includes both the species and its variety *sericeum;* "hypanthium *usually* more or less pubescent." The seventh edition of Gray's Manual goes further: "calyx white-tomentose." Study of material in the herbarium of

* Bull. Torrey Club **24**: 25. 1897.
† Bull. Torrey Club **24**: 570. 1897.
‡ Contr. U. S. Nat. Herb. **6**: 658. 1901.
§ Fl. SE. U. S. 894. 1903.

the New York Botanical Garden led to the conviction that *Vaccinium melanocarpum* of Gray's Manual is a good species, but that it is not identical with Mohr's species but with his variety *sericeum* only. On all sheets in the New York herbarium the character of pubescence on the hypanthium, always more or less definitely present on fruit as well, was accompanied by another character. The calyx lobes were accrescent in late flower or early fruit. This was easily evident to the eye, but on measuring, the balance of difference proved slight, the fruiting calyx being 1.5–2 mm. long in *P. stamineum* and 2.5–3 mm. long in the collections referable to *sericeum*. There was a single plant in which a glabrous hypanthium was accompanied by an accrescent calyx. This plant, on fine division, would be referred to *P. candicans* Small.

Examination of material from the United States National Herbarium shows that the same is true of the collections there. But the specimen that Mohr seems to have considered as the type of his species has a glabrous hypanthium, and the calyx is not accrescent. So far, then, as *Polycodium melanocarpum* (C. Mohr) Small is concerned, there is room for difference of opinion; if the character of succulent fruit is considered sufficient, it may be maintained as a species, but no other sufficient reason has been found for holding it specifically distinct from *P. stamineum*. But the evidence is otherwise as regards *V. melanocarpum sericeum*.

Typical forms of *P. candicans* (C. Mohr) Small differ notably from more typical *P. stamineum* in glaucescence, but the extremes are united by many intermediates, and no sharp line for separation has been found. Moreover, there is much reason for believing that this is a revival of *P. elevatum* Greene, the *Vaccinium album* of Pursh, although not the Linnaean species of the latter name, which does not belong to the family.

Two species have not been discussed, *P. oblongum* Greene and *P. Langloisii* Greene, of neither of which I have seen the types. Its author places the former in the *P. floridanum* group, but from the description and study of material which seems to match it I am inclined to refer it to *P. stamineum*, to which also *P. Langloisii* seems too closely related.

The following new combinations give effect to conclusions already stated.

Polycodium Kunthianum (Klotzsch) comb. nov.

Vaccinium stamineum β H. B. K. Nov. Gen. & Sp. **3**: 267. 1819.
Vaccinium elevatum β Dunal, in DC. Prodr. **7**: 568. 1839.
Picrococcus elevatus β Nutt. Trans. Am. Philos. Soc. II. **8**: 262. 1843.
Vaccinium Kunthianum Klotzsch, Linnaea **24**: 56. 1851.

Polycodium sericeum (C. Mohr) comb. nov.

Vaccinium melanocarpum sericeum C. Mohr, Contr. U. S. Nat. Herb. **6**: 658. 1901.
Vaccinium melanocarpum Robinson & Fernald, in Gray, Man. ed. 7. 639. 1908. Not *V. melanocarpum* C. Mohr, 1897.

NEW YORK BOTANICAL GARDEN.

INDEX TO AMERICAN BOTANICAL LITERATURE

(1912)

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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